Courtship Behavior of *Scaptomyza (Bunostoma) australis* Malloch

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There is general agreement that courtship in the Drosophilidae involves an exchange of information between the males and females and that during this exchange the female is released from inhibitions by the male (Grossfield, 1972). Differences in opinion do exist, however, concerning the actual intersexual interactions and the stimulus modalities involved in the exchange of information (Grossfield, 1972; Averhoff and Richardson, 1974; Petit and Nouaud, 1975; Bennet-clark *et al.,* 1976, Averhoff and Richardson, 1976; Ehrman and Parsons, 1976). Research to date has centered primarily on the examination of species representing one subgenus (Sophophora) of the genus *Drosophila.* The members of that subgenus possess a somewhat elaborate courtship pattern and, hence, a complex array of potential information exchange interactions even during the early portion of courtship. It is not surprising then that attempts to pinpoint the stimulus modalities involved in the intersexual information exchange during initiation and early courtship have led to disagreement. This is especially true since the two species involved in that research *(Drosophila melanogaster* Meigen and *D. pseudoobscura* Frolova) are both capable of integrating stimuli from different sensory inputs (Grossfield, 1971).

The genus *Scaptomyza,* which is closely related to *Drosophila* (Throckmorton, 1975), displays a generally simple courtship pattern when viewed in relation to members of the genus *Drosophila* (Sturtevant, 1921; Carson *et. al.,* 1970). In the present work we describe the courtship of one member of this genus, subgenus Bunostoma, *(S. australis).* We also present evidence on the stimulus modalities involved in intersexual information exchange and demonstrate that the use of a simple system to generate a baseline model can provide valuable insight on the mechanisms and stimulus modalities involved in early components of courtship of the Drosophilidae. The description here is the first detailed account of courtship in the genus *Scaptomyza.*

Materials and Methods

Scaptomyza (Bunostoma) *australis* Malloch was collected in August 1974 by aspirating adults from the interstices of fallen, partly rotted

apples in an orchard 20 km. from Melbourne in Victoria, Australia. Stocks were established and maintained on a cornmeal-agar medium at 20°C on a 12:12 light:dark cycle. In addition to observations on field caught specimens, virgin females and males were collected and stored separately in 8 dram food vials. These individuals were aged for 3 to 15 days before courtship observations were made.

Courtship was observed in food vials, beeswax chambers and plastic cells (18mm diameter by 6mm deep; Cook, 1973) at 20°C. Densities from two to twelve flies were observed at sex ratios of 1:1 and 2:3 (females:males). Neither of these variables altered the courtship pattern. A total of over 80 flies were observed in 16 observation periods ranging from 30 minutes to 4 hours. In addition, four sets of 3 males with 2 "headless" females were studies (see Grossfield, 1972 for procedural details).

Results

Courtship: The male positions himself behind another individual, with his long body axis in line with that of another fly. This behavior is initiated by the male detecting the movement of another individual and he achieves his oriented position by a series of stereotyped movements termed *tracking.* The precise pattern of the tracking behavior depends on the relative position and direction of movement of the tracked individual.

Tracking involves a set of coordinated, step-wise two-component body movements by the male. His head, pivoting at the neck, follows the moving individual through an arc. After the head passes through the maximum possible excursion of the arc, delineated by one side of the head contacting the anterior portion of the thorax, the body is realigned so that the head and body are on the same long axis. In some cases, depending on the direction and speed of movement of the tracked individual, there is a pause between the attainment of the maximum excursion and the realignment of the body. The logical inference from such pauses is that the detection of movement is being integrated across the surface of the eye (Gotz and Wenking, 1973). The two-stage tracking, with the aforementioned pauses, is continued, with some lateral displacement of the entire body, until the male is positioned behind the tracked individual with his long body axis in line with that of the other fly. The tracking is sometimes (15%, N = 34) preceded by a slow *waving* of one or both forelegs.

When the proper orientation is achieved, the male rushes to the rear of the tracked individual. If that individual continues moving the male follows and maintains the same orientation. If the individual stops, without turning, the male mounts and attempts to intromit. (Receptive females do not spread their wings prior to being mounted.) No attempt to mount a moving individual was observed

and non-receptive females may continue moving for varying periods of time (12 minutes in one case). Nonreceptive females being pursued were observed to depress the rear of the abdomen, extrude the ovipositor plates, or turn and fend (see below). Mounted non-receptive females were observed to depress and to dislodge the male with violent kicking. Males being pursued were observed to turn and fend (see below) and if mounted immediately dislodged the other male with violent kicking.

During copulation, the male's head is under the female's wings and the female is still. Usually, his forelegs are on the second tergum his midlegs are on the fourth tergum and his hindlegs are held around the venter. Alternately, the midlegs may be held around the venter and his hindlegs are on her hindlegs. His hindlegs may slip onto the substrate and he immediately repositions them. This may be repeated several times. At the end of copulation, the male withdraws and steps off without turning. The female immediately runs away. Twelve copulations were timed to yield a mean duration of 1 minute 58.9 seconds ± 5.1 seconds. Males and females were observed to copulate more than once during a 30 minute observation period.

Fending. Males, when face to face, rear up on their midlegs and hindlegs and fend with their forelegs. Males and females display a similar behavior when face to face and may even get the forelegs entangled for several seconds at the tibia-femur joint. Females, when face to face, rear up slightly and display a crab-like motion with the forelegs. In all situations the foreleg movements are slow and exaggerated.

Headless Female Studies: The use of headless females in courtship studies has been shown to provide data on intersexual information exchange and attendant stimulus modalities (Grossfield, 1972). Thus, observations of courtship involving headless females as well as observations on the general behavior of such females have been included in this study. Within minutes of decapitation, *S. australis* females twitch their legs and right themselves. They do not display any spontaneous locomotion nor do they locomote in response to external stimuli. They do respond to tactile stimulation with a slow crablike fending. They respond to directed air currents and chalk dust with preening. All parts of the body are preened including the "head". Some preening was observed which was apparently spontaneous in origin. Eighteen of 20 headless females were still living after 24 hours and 9 were still living after 48 hours.

In the observation cells with males, headless females again displayed no locomotion. The males approached these females and often tapped them but no tracking or mounting of these females was observed. The females respond to male contact with fending and preening. This tapping may bear no relationship to courtship in this species in that males were observed to tap numerous non-moving

objects which they encountered. Further, tapping was never observed to precede tracking or successful copulation.

While in the observation cells with headless females, males were observed to track, pursue and attempt to mount each other in response to movement. Demonstration that the males were heterosexually active in this situation was achieved by introducing a normal female. Within minutes, the *moving,* normal female was tracked pursued and mounted. All of the individuals from the observation cells were placed in food vials after the observation period. After 24 hours, the females were dissected; all of the normal females contained sperm but none of the headless females had been inseminated. The above observations are all consistent with the postulate that movement (from locomotion) is necessary to elicit male tracking behavior and the subsequent components of courtship.

Discussion and Conclusions

The courtship behavior of *Scaptomyza australis* is clearly initiated by movement. The ensuing courtship pattern consists of a two-stage tracking process followed by pursuit. When movement ceases, the male mounts and attempts to intromit. The head movement followed by body alignment to the tracked individual is an invariant component of this courtship.

Previous reports of courtship behavior in *Scaptomyza* include studies of North American and Hawaiian species (Sturtevant, 1921; Spieth, 1966). The North American species (*S.* (Mesoscaptomyza) *adjusta* (Loew) and *S.* (Scaptomyza) *graminum* (Fallen)) have been described as showing "very little courtship" all of which is directed at the female from the rear and includes some wing vibration and scissoring by the male. Mounting in these species occurs after genital contact (Sturtevant, 1921). Most of the Hawaiian species also incorporate some wing movement but, in contrast to the North American species, males mount before making genital contact (Spieth, 1966). If the genus *Scaptomyza* evolved as an offshoot of the *Drosophila* in Hawaii as hypothesized by Throckmorton (1975), then *S. australis* would represent a line in the evolution of this genus which has lost wing movement completely in courtship but retains the mounting-preceding-intromission sequence of the Hawaiian stem population. Thus, *S. australis* represents a lineage whose expressed courtship is the simplest yet known in *Scaptomyza.*

Relative to members of the genus *Drosophila,* the courtship pattern of *S. australis* from initiation through mounting is comparatively simple. That is, none of the complex components so common in *Drosophila* (i.e. licking, wing displays, and movements involving the proboscis, antennae and foretarsi) occur during this period of courtship in *S. australis.* There could be components of *Scaptomyza* court-

ship and intersexual information exchange which are not present in *Drosophila.* These might be related to the more complex genital structure of male *Scaptomyza* (Throckmorton, 1975). Such structural complexity could provide intersexual information and afford the female post-mounting discrimination capabilities. It is clear, however, that such capabilities are possible only after mounting occurs. It should be recalled that tracking and pursuit did not always result in mounting in this species. Thus, the period of courtship preceding attempted intromission remains of prime importance for considerations of intersexual information exchange. During that period the courtship pattern of *S. australis* is simpler than that of the *Drosophila* species used to date to study intersexual information exchange.

Averhoff and Richardson (1974) postulated that in *Drosophila melanogaster* intersexual information transfer is necessary for male "turn-on" and the initiation of courtship. Further, they suggested that the information is mediated through pheromonal channels. The evidence presented here for a simple drosophilid pattern indicates that movement is a necessary component of the information transfer involved in the initiation of courtship. The most obvious inference is that the stimulus modality involved is vision. However, a peromonal channel can not be immediately ruled out as the stimulus modality for the initiation of courtship since it is possible that pheromones are produced in this species. Movement could enhance the production, emission or direction of diffusion of a pheromone. If a pheromonal channel is involved in the initiation of courtship *directed* at an individual then, for males, *intra*sexual information is as effective as *inter*sexual information.

Two lines of evidence are inconsistent with peromonal mediation of male courtship initiation. Tracking behavior, which is elicited only by movement, is immediate, rigidly stereotyped and precise. Given these constraints on the attendent stimulus modality and the small size of the observation cell (which would become rapidly permeated with pheromones), it appears that a visual channel mediates the initiation of courtship and the tracking behavior (cf. Wehrhahn and Poggio, 1976).

The second line of evidence is also consistent with a visual channel mediating the initiation of courtship. A single male was placed in a meticulously cleaned observation cell with a small ball of clean cotton. Undisturbed for 30 minutes, the male walked about the cell and occasionally preened. When the cell was rocked so that the cotton ball moved, the male immediately began stereotyped tracking behavior and, when the appropriate orientation had been achieved, pursuit. When the rocking ceased, so did tracking. This was invariantly repeatable. No mounting with the cotton ball was observed nor was tracking observed when a cell containing only a male was rocked.

It would appear, then, that the initiation of courtship in males is activated by movement and mediated through visual channels in this drosophilid. The visual tracking ability and the involvement of vision in the very early stages of courtship is not surprising in light of the results obtained in measurement of the visual orientation capability and control mechanisms demonstrated in laboratory tests of Diptera (Wehrhahn and Poggio, 1976). This is, however, the first report of this fine a degree of control of visual orientation obtaining during sexual behavior. It must be pointed out that the visual mediation demonstrated here is reflective of sighted flies tested in the light. Whether this species is capable of switching to a different stimulus modality when deprived of vision (heteromodal behavioral plasticity) is not known but is under investigation. Several species of the Drosophilidae are known to possess such capabilities (Grossfield, 1971).

The study of courtship in the Drosophilidae has included analysis of behavioral mechanisms (Connolly and Cook, 1973) as well as comparative studies with a view towards evolutionary relationships (Spieth, 1966). The examination of courtship of a species in this family with a simple courtship repetoire provides a baseline model for intersexual interaction which may provide a more precise evaluation of the various information transfer mechanisms involved in the more complex courtship patterns of other members of this family.

Acknowledgements

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